THREATS TO THE CALIFORNIA FLORA: UNGULATE GRAZERS AND BROWSERS

ELIZABETH L. PAINTER
Jepson and University Herbaria,
University of California, Berkeley, CA 94720

ABSTRACT

While herbivory probably is a natural part of all terrestrial ecosystems, livestock herbivory is not a natural part of California's natural ecosystems. In California, mammalian herbivores can range in size from small rodents to large ungulates. However, the potential of threats is greater from ungulates, which include native taxa (e.g., tule, Roosevelt, and Rocky Mountain elk, mule deer, pronghorn antelope) and alien livestock (e.g., cattle, horses, burros, sheep, goats). Impacts of the native ungulates are not well studied. There are few, if any, types of plant communities in California that are unimpacted by livestock. Livestock herbivory is a threat to some rare plant taxa. Livestock impacts can include alterations in species composition of plant communities, in ecosystem function, and in ecosystem structure. Although the impacts can be severe, in terms of negative impacts on native plants, carefully managed livestock herbivory may not be the most destructive land use practice.

Herbivory is a natural part of most (if not all) ecosystems. However, not all herbivory is equivalent and activities of different species of herbivores produce very different effects. Few people would expect the effects of grazing activities of grasshoppers and bison to be similar, but it is less obvious that even two superficially similar grass specialists, such as bison and cattle, use the landscape differently, feed on different plant species, have different digestive efficiencies, etc. There are no simple substitutions among taxa.

In California, mammalian herbivores can range in size from small rodents to large ungulates. Although small mammals do impact and sometimes significantly alter their environment (e.g., Cox 1984, 1986, 1990, Hobbs and Hobbs 1987, Hobbs and Mooney 1985, Koide and Mooney 1987), the potential of threats is greater from larger animals.

There is limited consensus as to the effects of ungulate herbivory. There is not even agreement on definitions of terms. As one scans the "grazing" literature, one finds "to graze" is used to mean (1) any type of consumption of aboveground production of both woody and herbaceous plants (not just fruits or seeds), (2) to feed primarily on herbaceous plants, or (3) to feed primarily on grasses or graminoids (Poaceae, Cyperaceae, Juncaceae). "To browse" is used to mean to feed primarily on (1) woody plants or (2) nongrasses or nongraminoids. A statement such as "grazing is a natural process on all plant

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communities" (Box and Malechek 1987) takes on different meanings, depending upon the definition used. Both "browse" and "graze" may be used only for defoliation or may include some or all ancillary impacts (e.g., trampling, excrement, pull-up and breakage). In this paper, I am using definition 2 of "graze" (to feed primarily on herbaceous plants), definition 1 of 'browse' (to feed primarily on woody plants), and 'herbivory' for a combination of the two. I am including ancillary impacts with all three terms. These categories are generalizations; "animals are neither plant taxonomists nor community ecologists and consume plants according to [plant] availability and [the animal's] preference" (Huston and Pinchak 1991).

Large ungulates in California include native taxa (e.g., tule, Roosevelt, and Rocky Mountain elk, mule deer, pronghorn antelope) and aliens (e.g., cattle, horses, burros, sheep, goats)—a mixture of grazers, browsers, and facultative browser/grazers. The native ungulates are facultative browser/grazers or browsers, rather than grazing specialists like cattle (Murie 1951, Vallentine 1990).

There have never been modern plains bison (a grazer) in what is now California (McDonald 1981, D. Van Vuren, personal communication). The extinct prehistoric bison were quite different in morphology, habitat preference, and probably in herding behavior, since (like the modern European bison and the Canadian wood bison) they were browsers or browser/grazers, and probably did not congregate in large herds (McDonald 1981).

Before European settlement, there were three elk taxa (tule, Roosevelt, Rocky Mountain), with different ranges and habitat preferences, although their ranges apparently did overlap slightly in northern California and there apparently was some hybridization (C. Schonwald-Cox, personal communication). Roosevelt elk lived along the north coast, in places similar to Prairie Creek Redwoods State Park. Tule elk were found in drier areas than Roosevelt elk, inhabiting much of the oak woodland and savanna, primarily in and around the Central Valley. Tule elk are not native to some areas where they live in reserves today, (e.g., Point Reyes National Seashore). Rocky Mountain elk were found only in extreme northeastern California. Elk are highly versatile and opportunistic in diet choice, utilizing a broad range of herbaceous and woody vegetation (Murie 1951, Jenkins and Starkey 1991). Grasses can be an important component. Mule deer were found in woodlands, savannas, riparian zones, and post-burn chaparral. They are seasonally facultative browser/grazers, utilizing more herbaceous plants during the growing season and more woody plants during the rest of the year (Vallentine 1990). Pronghorn were found in drier, more open habitats, including desert habitats. They are browers, and grass is only a minimal part of their diets (Vallentine 1990).

In California, there are quite a few alien ungulates, both domestic

livestock and feral animals descended from livestock. Domestic livestock include sheep, goats, horses, burros, and cattle. Occasionally they also include ungulates native to California but not to the local area (e.g., elk and deer on Santa Rosa Island). Feral ungulates include burros, horses, sheep, and goats. Management regimes designed to remove feral animals or to minimize their impacts vary with species and location, and success has also varied. Feral horses and burros are protected by law, so only live removal is permitted. Because live removal is difficult, sheep and goats are usually killed. However, killing has upset animal-rights groups and has been stopped in some areas. Burros, horses, and sheep are grazers or browser/grazers (depending on habitat), and goats are browsers or browser/grazers (Vallentine 1990). Cattle are grazers and, whenever possible, cattle feed primarily on grasses (Vallentine 1990).

In North America, the effects of native ungulates on plants in their native habitats have not been well studied, except for a few areas in the Great Plains (e.g., Wind Cave National Park, see Holland et al. 1992, Painter et al. 1993, Whicker and Detling 1988, and literature therein). There have been no such intensive studies in California.

Recently, both the scientific and popular literature have published debates about benefits and costs of alien ungulate (livestock) grazing in western North America (see Belsky 1986, 1987, Painter and Belsky 1993 for bibliography). *Fremontia* (California Native Plant Society) has published a number of articles and letters (Baker 1992, Barrett 1992, Belsky 1992, Blumler 1992, Edwards 1992a, b, 1993, Keeley 1993, Menke 1992, Stebbins 1992). There are those who strongly believe that plants and ecosystems of western North America benefit from livestock herbivory, that herbivory may be necessary to sustain the system, and that livestock are just tools (e.g., Goetz 1994, Hill 1991). Others strongly oppose these ideas (e.g., Jacobs 1991, Wuerthner 1994a, b). While there is an enormous body of literature on livestock herbivory in western North America, most of it concerns increasing livestock production or increasing forage production to feed livestock. Comparatively little research has been designed to examine what happens when livestock are removed. Nongrazed land is relatively rare, and most areas that are livestock-free are too small for valid comparisons (Bock et al. 1993). Effects of livestock may be greater west of the Rocky Mountains than on the Great Plains (Mack and Thompson 1982). Ecological costs of livestock in western North America can be dramatic (Fleischner 1994).

The impacts of livestock on plants vary, depending on animal species, numbers, and management. Both feral and domestic livestock can have significant negative impacts on plant taxa, plant communities, and ecosystems.

Individual plants can be impacted directly, by defoliation, pull-

up, breakage and trampling, or indirectly, by animal-induced changes in habitat, changes in competitive relationships among plants, destruction of seedlings, or changes in conditions so that seeds don't germinate, etc. Impacts on juveniles may be greater than on adults, greatly reducing or eliminating reproductive success. Long-lived taxa whose reproduction has been impacted by herbivores may now persist primarily through inertia (*sensu* Cole 1985). While nondefoliated plants may benefit from reduced competition from defoliated plants, there is no compelling evidence that individual plants benefit from being defoliated (Belsky 1986, Painter and Belsky 1993). Among the 1742 plant taxa listed by the California Native Plant Society as rare, threatened, or endangered, at least 225 taxa to some degree are "threatened by grazing" (Skinner and Pavlik 1994).

Livestock herbivory does not have equally negative effects on all native plants. Some plants apparently can tolerate a certain amount of herbivory; others have avoidance mechanisms. This resistance (avoidance/tolerance) to herbivory has been interpreted by some (e.g., Edwards 1992) as an adaptation to grazing. It is more probable that the resistance is a strategy to reduce the negative impacts of all types of damage (Belsky et al. 1993). Plants experience injury from a wide variety of sources besides herbivory, including fire, wind, and freezing. Plants often have similar responses to damage from several different sources. This is not the same as being 'adapted' to ungulate herbivory. Resistance to damage is not necessarily predictable. It can vary among closely related species, and even between populations of the same species (e.g., Painter et al. 1989, 1993). Some native California plant species appear to have limited tolerance of livestock grazing. However, if they are preferred foods, the resulting stress may put them at a competitive disadvantage with unpalatable plant species and with more grazing tolerant species, leading to a decline in number or even a loss from the community. However, in many areas, they appear to have been able to persist, in reduced numbers and sizes of plants, although often with little reproduction from seed. Since there is very little information available about the lifespan of these taxa, it is not known how long inertia will be enough to maintain their presence.

There are few, if any, types of plant communities in California that are unimpacted by livestock. Impacts of livestock can be found even on beaches and dunes (e.g., on Santa Rosa Island, personal observation). Intensive use by livestock (feral or domestic) has had adverse effects on many pine and cypress communities (Vogl et al. 1990). Effects of livestock on oak woodlands and savannas are equivocal (Griffin 1990). Although climate and native herbivores are often important, livestock can have a role in reducing oak regeneration. The invasion of oak communities by alien plants also appears to be related to the introduction of livestock. Oaks were more plentiful

before European-American settlement. Habitat was lost to cultivation, and many oak stands were eliminated or thinned to increase forage for livestock. Areas that are open woodlands were once more closed, savannas were woodlands, and grasslands were savannas. Communities now dominated by alien annual grass taxa probably owe their origin to livestock (Baker 1978, Heady 1990). Wetlands are especially attractive to livestock and therefore often are more heavily impacted than other nearby communities (Heady and Child 1994, Vallentine 1990). Livestock concentrate their activities in riparian areas, around margins of permanent lakes and ponds, and in and around vernal wetlands. Impacts on mountain meadows can remain visible for decades after livestock use has been terminated (Rundel et al. 1990). Livestock can affect the balance between community types along ecotones, e.g., coastal-prairie/coastal-scrub, sagebrush-steppe/conifer-woodland, and sagebrush-steppe/grassland (Heady et al. 1990, Young et al. 1990). Pinyon-juniper woodlands have been treated (trees poisoned or mechanically removed) to enhance forage for livestock (Evans and Young 1987), a process that does not necessarily enhance the habitat for other native plant taxa. Heavy livestock use has changed community composition and structure in some desert communities (Fleischner 1994, Vasek and Barbour 1990).

Livestock herbivory can lead to alterations in species composition of plant communities, ecosystem function, and ecosystem structure (reviewed in Fleischner 1994). Altered species composition can include decreases in densities and diversity of native plant taxa, changing a shrub-dominated community into a grass-dominated one or vice versa. Livestock can destabilize plant communities by aiding the spread and establishment of alien plant taxa, both by transporting seeds and by creating habitat for disturbance-loving alien ruderals. Changes in a plant community affect the animal community (e.g., lack of food and/or cover changes the rodent community, which impacts the predators, etc.). Ecosystem function may be altered through changes in nutrient cycles, water cycles, etc. Livestock grazing always results in a net loss of nutrients, since livestock are exported rather than decomposing in place. In addition, at least some areas in California, like many areas west of the Rocky Mountains, lack organisms necessary for decomposition and recycling of nutrients tied up in cattle and horse feces (see Mack and Thompson 1982). Dried, apparently intact feces can be found several years after removal of livestock (personal observation). Alteration in ecosystem structure can include changes in vegetation stratification, increases in soil compaction, and loss of soil stability (Fleischner 1994). Loss of plant cover, soil crusts, and litter can increase loss of soil to erosion. Loss of plant cover, together with decreased water infiltra-

tion (related to soil compaction) can contribute to flooding and gullying. Cryptobiotic soil crusts are essential to ecosystem function and structure in semi-arid and arid ecosystems (Fleischner 1994). These crusts are composed of cyanobacteria, lichens, and mosses, and are associated with increased organic matter, available phosphorus, increased soil stability, increased soil moisture, and enhanced seedling establishment. Cyanobacteria (both free-living and in lichens) fix nitrogen, and can be the dominant source of this limiting nutrient in arid systems. Livestock trampling can greatly damage or destroy these crusts.

Livestock are allowed on public lands in California, on federal, state, regional, county, municipal properties, from national parks to municipal watersheds. Nearly 45% of California is federal land (Jacobs 1991). Environmental Assessments and/or Environmental Impact Studies are often required before grazing can be initiated on public lands and before expired leases can be renegotiated. Such documents need to be carefully reviewed by an informed public. While many are well written, well researched documents, others base management plans on popular (but scientifically unsubstantiated) concepts (e.g., Savory 1988).

In terms of negative impacts on native plants, livestock herbivory may not be the most destructive land use practice. There are a lot fewer native plants in cultivated fields and manicured lawns than in grazed savannas. Although it is not true for most of the western United States, in the more desirable parts of California much of what is now used for livestock might be lost to subdivisions and development—sometimes the choice is cows or condos (see Wuerthner 1994c).

Careful consideration of alternative land uses needs to be made before an end to grazing is called for. Many of the negative impacts of grazing can be mitigated with careful, well planned management. In areas where livestock herbivory is going to continue, selection for damage tolerance might allow for increased success in revegetation with natives. All management decisions have consequences. Abrupt changes in livestock herbivory can bring new problems, e.g., a major increase in *Foeniculum vulgare* on Santa Cruz Island when cattle were removed (Junak et al. 1995).

While herbivory probably is a natural part of all terrestrial ecosystems, livestock herbivory is not a natural part of California natural ecosystems. Livestock behavior does not mimic that of either Pleistocene or modern native California herbivores (Baker 1992). It must be viewed as a human-imposed alien disturbance and be carefully managed to minimize negative impacts. That said, there is a place for carefully managed livestock in California, particularly on private land. The livestock industry is significant both economically

and culturally, and, if carefully managed, it can help maintain open space and a place for much of the native flora that would be lost with other land uses.

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Literature cited

Baker, H. G. 1978. Invasion and replacement in Californian and neotropical grasslands. Pp. 368–384 *in* J. R. Wilson (ed.), Plant Relations in Pastures, CSIRO, Melbourne, Australia.

———. 1992. Letter to the editor. Fremontia 20(3):32–33.

Barrett, R. H. 1992. Letter to the editor. Fremontia 20(3):29–30.

Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. American Naturalist 127:870–892.

———. 1987. The effects of grazing: confounding ecosystem, community, and organism scales. American Naturalist 129:777–782.

———. 1992. Letter to the editor. Fremontia 20(3):30–31.

———, W. P. Carson, C. J. Jensen, and G. A. Fox. 1993. Overcompensation by plants: herbivore optimization or red herring? Evolutionary Ecology 7:109–121.

Blumler, M. A. 1992. Some myths about California grasslands and grazers. Fremontia 20(3):22–27.

Bock, C. E., J. H. Bock, and H. M. Smith. 1993. Proposal for a system of federal livestock exclosures on public rangelands in the western United States. Conservation Biology 7:731–733.

Box, T. W. and J. C. Malechek. 1987. Grazing on the American rangelands. Volume 38, Proceedings, Annual Meeting, Western Section, American Society of Animal Science. Utah State University, Logan, UT.

Cole, K. L. 1985. Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. American Naturalist 125:289–303.

Cox, G. W. 1984. The distribution and origin of mima mound grasslands in San Diego County, California. Ecology 65:1397–1405.

———. 1986. Mima mounds as an indicator of the presettlement grassland-chaparral boundary in San Diego County, California. American Midland Naturalist 116:64–77.

———. 1990. Soil mining by pocket gophers along topographic gradients in a mima moundfield. Ecology 71:837–843.

Edwards, S. W. 1992a. Letter to the editor. Fremontia 20(3):31–32.

———. 1992b. Observations on the prehistory and ecology of grazing in California. Fremontia 20(1):3–11.

———. 1993. Letter to the editor. Fremontia 22(2):27.

Evans, R. A. and J. A. Young. 1987. Control, plant succession, and revegetation. Pp. 301–321 *in* R. L. Everett (compiler), Proceedings—Pinyon-Juniper Conference. General Technical Report INT-215. U.S.D.A. Forest Service Intermountain Research Station, Ogden, UT.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629–644.

Goetz, H. 1994. Letter to the editor. Rangelands 16:44–45.

Griffin, J. R. 1990. Oak woodlands. Pp. 383–415 *in* M. G. Barbour and J. Major (eds.), Terrestrial Vegetation of California. California Native Plant Society Special Publication No. 9.

HEADY, H. F. 1990. Valley grassland. Pp. 491–514 *in* M. G. Barbour and J. Major (eds.), Terrestrial Vegetation of California. California Native Plant Society Special Publication No. 9.

——— and R. D. CHILD. 1994. Rangeland Ecology and Management. Westview Press, Boulder, CO.

———, T. C. FOIN, M. M. HERTNER, D. W. TAYLOR, M. G. BARBOUR, and W. J. BARRY. 1990. Coastal prairie and northern coastal scrub. Pp. 733–760 *in* M. G. Barbour and J. Major (eds.), Terrestrial Vegetation of California. California Native Plant Society Special Publication No. 9.

HILL, A. 1991. Grazing as a management tool. Wildflower 4(1):13–18.

HOBBS, R. J. and V. J. HOBBS. 1987. Gophers and grassland: a model of vegetation response to patchy soil disturbance. Vegetatio 69:141–146.

——— and H. A. MOONEY. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. Oecologia (Berlin) 67:342–351.

HOLLAND, E. A., W. J. PARTON, J. K. DETLING, and D. L. COPPOCK. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. American Naturalist 140:685–706.

HUSTON, J. E. and W. E. PINCHAK. 1991. Range animal Nutrition. Pp. 27–63 *in* R. K. Heitschmidt and J. W. Stuth (eds.), Grazing Management: An Ecological Perspective. Timber Press, Portland, OR.

JACOBS, L. 1991. Waste of the West: Public Lands Ranching. Lyn Jacobs, Tucson, AZ.

JENKINS, K. J. and E. E. STARKEY. 1991. Food habits of Roosevelt elk. Rangelands 12:261–265.

JUNAK, S., T. AYERS, R. SCOTT, D. WILKEN, and D. YOUNG. 1995. A Flora of Santa Cruz Island. Santa Barbara Botanic Garden and California Native Plant Society (in press).

KEELEY, J. E. 1993. Letter to the editor. Fremontia 21(1):29.

KOIDE, R. T. and H. A. MOONEY. 1987. Spatial variation in inoculum potential of vesicular-arbuscular mycorrhizal fungi caused by formation of gopher mounds. New Phytologist 107:173–182.

MACK, R. N. and J. N. THOMPSON. 1982. Evolution in steppe with few large hooved mammals. American Naturalist 119:757–773.

MCDONALD, J. N. 1981. North American Bison: Their Classification and Evolution. University of California Press, Berkeley.

MENKE, J. W. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. Fremontia 20(2):22–25.

MURIE, O. J. 1951. The Elk of North America. Stackpole Co., Harrisburg, PA.

PAINTER, E. L. and A. J. BELSKY. 1993. Application of herbivore optimization theory to rangelands of the western United States. Ecological Applications 3:2–9.

———, J. K. DETLING, and D. A. STEINGRAEBER. 1989. Grazing history, defoliation, and frequency-dependent competition: effects on two North American grasses. American Journal of Botany 76:1368–1379.

———, J. K. DETLING, and D. A. STEINGRAEBER. 1993. Plant morphology and grazing history: relationships between native grasses and herbivores. Vegetatio 106:37–62.

RUNDEL, P. W., D. J. PARSONS, and D. T. GORDON. 1990. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. Pp. 559–599 *in* M. G. Barbour and J. Major (eds.), Terrestrial Vegetation of California. California Native Plant Society Special Publication No. 9.

SAVORY, A. 1988. Holistic Resource Management. Island Press, Covello, CA.

SKINNER, M. W. and B. M. PAVLIK (eds.). 1994. California Native Plant Society's Inventory of Rare and Endangered Vascular Plants of California, 5th edition. California Native Plant Society, Sacramento, CA.

STEBBINS, G. L. 1992. Letter to the editor. Fremontia 20(3):31–32.

VALLENTINE, J. F. 1990. Grazing Management. Academic Press, Inc., San Diego, CA.

VASEK, F. C. and M. G. BARBOUR. 1990. Mojave Desert scrub vegetation. Pp. 835–867 *in* M. G. Barbour and J. Major (eds.), Terrestrial Vegetation of California. California Native Plant Society Special Publication No. 9.

VOGL, R. J., W. P. ARMSTRONG, K. L. WHITE, and K. L. COLE. 1990. The closed-cone pines and cypress. Pp. 295–358 *in* M. G. Barbour and J. Major (eds.), Terrestrial Vegetation of California. California Native Plant Society Special Publication No. 9.

WHICKER, A. D. and J. K. DETLING. 1988. Ecological consequences of prairie dog disturbances. BioScience 38:778–785.

WUERTHNER, G. 1994a. Letter to the editor. Rangelands 16:44.

———. 1994b. Letter to the editor. Rangelands 16:171–172.

———. 1994c. Subdivisions versus agriculture. Conservation Biology 8:905–908.

YOUNG, J. A., R. A. EVANS, and J. MAJOR. 1990. Sagebrush steppe. Pp. 763–796 *in* M. G. Barbour and J. Major (eds.), Terrestrial Vegetation of California. California Native Plant Society Special Publication No. 9.

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